Inheritance Patterns of Parthenocarpic Fruit Development in Highbush Blueberry (*Vaccinium corymbosum* L.)

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Abstract. **Forty-one half-sib families (>3000 individuals) segregating for parthenocarpic fruit production were evaluated under field conditions. Within these families, ≈280 parthenocarpic individuals were identified. In general, three categories of segregants were observed: normal-seeded types, small/low-seeded types, and parthenocarpic types. Inheritance patterns suggested that the trait is recessive, but did not fit simple tetrasomic recessive or incomplete dominance models. Lack of fit may be attributable to environmental interactions or incomplete penetrance of this trait. Further evaluations are underway with small/low-seeded types with the expectation that offspring of these plants may express the trait at higher frequencies than in $F_1 \times F_1$ crosses. The reduced vigor in many of the parthenocarpic segregants suggests that this germplasm will be most useful, initially, in improving fruit quality in the intermediate expression types, which have better fruit set and reduced seed development.**

Normal fruit development is initiated by gibberellins or auxins generated by the developing ovule. These compounds stimulate early fruit development and also promote fruit set (i.e., the prevention of abscission) (Crane, 1964). In some cases, parthenocarpy, the development of fruit without seed, may occur. In certain parthenocarpic types, pollination either does not take place or it does not result in fertilization and seed development. Natural parthenocarpy has been documented in various crops, including grape (Wong, 1941), tomato (Groot et al., 1987; Wong, 1941), mandarins (Talon et al., 1992), banana (Gustafson, 1939), and opuntia (Weiss et al., 1993). Furthermore, considerable work has been conducted on the induction of parthenocarpic fruit using growth regulators in a wide variety of horticultural crops either to study fruit development or to evaluate potential utilization in production. Among such crops are kiwifruit (Ohara et al., 1997), pepino (Ercan and Akilli, 1996), watermelon (Pak, 1993), pears (Yamada et al., 1991), grape (Fellman, et al., 1991), strawberry (Mudge et al., 1981), and cucumber (Kim et al., 1994a, 1994b).

In recent years, physiological and molecular studies have elucidated more completely the nature of parthenocarpic development in several target species. Parthenocarpic mutants of tomato have been studied more thoroughly than those of many other crops. In tomato, several single-gene recessives have been identified that control the character (Fos et al., 2001; Gorguet et al., 2005; Mazzucato et al., 1998). In contrast, in pepino (*Solanum muricatum*), a single-gene dominant has been implicated in genetic control (Prohens et al., 1998). Molecular and physiological studies of parthenocarpy have implicated involvement of genes as diverse as those controlling auxins and gibberellins (tomato) (Fos et al., 2001; Gorguet et al., 2005); and self-incompatibility, histones, and alcohol dehydrogenase (tomato) (Testa et al., 2002). Rotino et al. (1997) demonstrated the use of a transgenic IAA-m gene in tobacco and eggplant in inducing parthenocarpy. Several studies have suggested that parthenocarpy genes may also play a role in reproductive morphology (tomato anther development) (Mazzucato et al., 1998) and may play a critical role in early ovule development (watermelon) (Sedgley, 1979).

In blueberry, limited work has been done, but several groups have demonstrated that normal fruit development exhibits high levels of GA during early stages of development in both highbush and lowbush blueberries (Kender and Desroches, 1970; Mainland and Eck, 1968, 1971). Other studies have shown that parthenocarpy may be induced by GA_3 in cases of pollination failure (Cano-Medrano and Darnell, 1998; Mainland and Eck, 1969; Nesmith et al., 1995). Several authors have noted tendencies toward parthenocarpy in blueberry (i.e., some parthenocarpic fruit, low seed numbers, high pulp-to-seed ratios) (Ehlenfeldt, 2001; Ehlenfeldt and Hall, 1996; Harrison et al., 1994; MacKenzie, 1997).

Parthenocarpy in any fruit-bearing crop is a very desirable trait because it holds the possibility of reduced concerns about many typical pollination worries. In a crosspollinated crop like blueberry, parthenocarpy could address at least three pollination concerns: 1) suboptimal pollination weather during the bloom period, 2) declines of pollinators resulting from parasitic infections, and 3) desirability of crosspollination versus self-pollination for optimum yield.

G-176, a highbush selection (primarily *V. corymbosum* L.), was identified by Rutgers University among USDA breeding materials that appeared to set fruit parthenocarpically. This plant was valuable because it set fruit whether pollinated or unpollinated. Fruit from pollinated flowers was large and could have a small number of seed; unpollinated fruit was seedless. First-generation crosses of G-176 with normal phenotypes did not exhibit parthenocarpy, but parthenocarpy was recovered in half-sib families, suggesting this trait was recessive (Vorsa, unpublished data). This material, however, was in a poor phenotypic background and recovery of varietal quality types was difficult. This study presents a detailed examination of the inheritance of this trait and an evaluation of its potential for development.

Materials and Methods

A parthenocarpic variant, G-176, was discovered in highbush blueberry (*Vaccinium corymbosum* L.) (2n = 4x = 48) in a family of the pedigree G-105 × E-204. The female parent, G-105, was a cross of 11-93 (a 'Bluecrop' sibling) × 'Herbert'. The male parent, E-204, was a cross of E-7 ('Berkeley' × 'Earliblue') × F-72 ('Wareham' × 'Pioneer'). For this study, G-176 was crossed to a diverse selection of cultivars and clones to produce families from which F_1 parents were selected.

In 1993, studies evaluated four $F_1 \times F_1$ families generated from combinations of intercrosses of five F_1 hybrids of G-176 by standard highbush cultivars ('Bluecrop', 'Collins', 'Elizabeth', 'Elliott', and 'Jersey') and four backcross families of these hybrids to G-176. In these evaluations, two clusters of five or more fruit were collected from 4-year-old field-grown plants. Fruit was cut open equatorially and categorized as either seeded or parthenocarpic.

For the studies evaluated in 2004 and 2005, initial F_1 hybrids were generated from 10 field-grown families, and better-performing clones were selected and retained. Selected clones (based primarily on vigor and general productivity) (Table 1) were entered into half-sib crosses and the resulting progeny were planted to the field in several successive years. Backcrosses were also performed, but seed set was low and offspring were weak,

presumably attributable to inbreeding effects. When the progeny of these crosses were 3 years old, they were evaluated for expression of parthenocarpy. For evaluation, each fruiting clone had at least three fruit harvested and categorized. For evaluation, fruit was cut open equatorially and graded for seed production. Notes were taken of any other unusual variations. If a clone was found to be parthenocarpic, fruit from that clone and the clones on either side of it were recollected and rechecked to positively identify the correct clone and to verify the initial observation. In 2004, we evaluated 22 segregating half-sib families comprised of more than 2000 individuals. In 2005, we evaluated an additional 29 half-sib families comprised of more than 1100 individuals.

Segregation ratios were evaluated by χ^2 tests within the context of a single-gene recessive or an incomplete dominance model for duplex × duplex half-sib crosses. Data were also evaluated for possible duplex × simplex half-sib segregations, because it is possible that the variant gene existed as a masked recessive in "normal" parents resulting in a simplex rather than duplex composition in some F_1 parents.

Results and Discussion

Because other parthenocarpic mutants have been found to be under single gene control, we hypothesized that seeded types were $P - - -$ and parthenocarpic types were $pppp$. Under a tetrasomic model, a 35:1 segregation of normal:parthenocarpic would be expected in half-sib families and a 5:1 ratio in backcrosses (Fig. 1). In our crosses, this character behaved as a recessive. All F_1 hybrids appeared to have normal seed production if pollinated and no fruit set if unpollinated. The trait segregated in both $F_1 \times F_1$ crosses and $F_1 \times$ G-176 backcrosses. In 1993, we evaluated four half-sib families comprised of 149 individuals segregating for parthenocarpic fruit production. Among these families, five parthenocarpic individuals were identified. We also evaluated four backcross families comprised of 40 individuals and identified four parthenocarpic individuals (Table 2).

In 2004, we evaluated 22 half-sib families comprised of more than 2000 individuals, and among these families, 89 parthenocarpic individuals were identified. In the 2004 backcross family evaluations, two families, comprised of 77 individuals, produced seven parthenocarpic individuals (Table 3). In 2005, we evaluated an additional 29 half-sib families comprised of more than 1100 individuals. Among these families, 196 parthenocarpic individuals were identified. In the 2005 backcross family evaluations, four families, comprised of 62 individuals, produced nine parthenocarpic individuals (Table 3).

In reviewing notes of 2004 and 2005 evaluations, it was felt that three phenotypic classes could be recognized: normal-seeded types, diminished seed types, and parthenocarpic types (Fig. 2). In the diminished seed types, several features were noted: 1) reduced seed number, 2) reduced seed size, and 3) what appeared to be a relative increase in flesh development with a concordant decrease in the area of the pulp occupied by the seed. Consequently, these families were evaluated under two alternative sets of assumptions. Under the first model, plants were classified as seeded or parthenocarpic as before. Under the second model, we recognized the three classes—normal seed, diminished seed, and parthenocarpic—and hypothesized their genotypes to be $PP - -$, $Pppp$, and $pppp$, respectively. In this incomplete dominance model,

Table 1. F_1 hybrids used as parents of families assayed in 2004 and 2005 for parthenocarpy inheritance.

Selection	Pedigree	Comments on female parent
US 1015, US 1016	Bluetta × G-176	Early ripening
US 1017	Chandler × G-176	Late ripening, large fruit
US 1018	G 850 × G-176	Early ripening
US 1019, US 1020	US 880 × G-176	*V. boreale* derivative
US 1025, US 1041	Sunrise × G-176	Early ripening
US 1026	G 172 × G-176	Late ripening
US 1027	G 303 × G-176	Midseason ripening, large fruit
US 1028, US 1042	Toro × G-176	Midseason ripening, large fruit
US 1039	JU 62 × G-176	*V. myrsinites* × *V. angustifolium* selection
US 1040	NC 2909 × G-176	*V. elliottii* derivative

Table 2. Class data and χ^2 probabilities for half-sib and backcross families segregating for parthenocarpy in a single-gene recessive model in 1993.

	Recessive model			
Cross	Seeded	Parthenocarpy	χ^2 prob. duplex × duplex	χ^2 prob. duplex × simplex
Half-sib crosses				
NJ 90-225 (Jersey × G-176) × (Bluecrop × G-176)	17	0	0.49	0.21
NJ 90-234 (Collins × G-176) × (Elizabeth × G-176)	43	2	0.50	0.35
NJ 90-248 (Elliott × G-176) × (Bluecrop × G-176)	54	1	0.67	0.08
NJ 90-240 (Elliott × G-176) × (Bluecrop × G-176)	30	2	0.23	0.67
Half-sib total	149	5 ($\approx$30:1)	0.72	0.02
Backcrosses				
NJ 91-505 (Jersey × G-176) × G-176	12	0	0.12[z]	< 0.01[z]
NJ 91-508 (Bluecrop × G-176) × G-176	12	2	0.81	0.04
NJ 91-513 (Jersey × G-176) × G-176	6	1	0.87	0.15
NJ 91-500 (Collins × G-176) × G-176	6	1	0.87	0.15
Backcross total	36	4 (9:1)	0.26	< 0.01

[z]Models tested in backcrosses are duplex × nulliplex and simplex × nulliplex crosses, respectively.

		Seeded	Diminished	Parthenocarpic
Single gene recessive model				
F_2 - duplex x duplex	$PPpp$ x $PPpp \longrightarrow$	1 $PPPP$: 8 $PPPp$: 18 $PPpp$: 8 $Pppp$		1 $pppp$
F_2 - duplex x simplex	$PPpp$ x $Pppp \longrightarrow$	1 $PPPP$: 5 $PPpp$: 5 $Pppp$		1 $pppp$
Backcross – duplex x nulliplex	$PPpp$ x $pppp \longrightarrow$	4 $PPpp$: 1 $Pppp$		1 $pppp$
Backcross – simplex x nulliplex	$Pppp$ x $pppp \longrightarrow$	1 $Pppp$		1 $pppp$
Incomplete dominance model				
F_2 - duplex x duplex	$PPpp$ x $PPpp \longrightarrow$	1 $PPPP$: 8 $PPPp$: 18 $PPpp$	8 $Pppp$	1 $pppp$
F_2 - duplex x simplex	$PPpp$ x $Pppp \longrightarrow$	1 $PPPP$: 5 $PPpp$	5 $Pppp$	1 $pppp$
Backcross – duplex x nulliplex	$PPpp$ x $pppp \longrightarrow$	4 $PPpp$	1 $Pppp$	1 $pppp$
Backcross – simplex x nulliplex	$Pppp$ x $pppp \longrightarrow$		1 $Pppp$	1 $pppp$

Fig. 1. Genotypic outcomes for alternative single-gene F_2 and backcross models of parthenocarpy under tetrasomic inheritance.

Table 3. Class data and χ² probabilities for half-sib and backcross families (grouped by female parent) segregating for parthenocarpy in 2004 and 2005 under single-gene recessive and incomplete dominance models.

Female parent	Recessive (r) model		Incomplete dom. (id) model			χ², duplex × duplex		χ², duplex × simplex[z]	
	Seeded	Parthenocarpy	Seeded	Dimin.	Parthenocarpy	r model	id model	r model	id model
2004 half-sib crosses									
US 1015 (1 family)	24	1	18	6	1	0.71	*0.97* (0.91*)[y]*	0.43	0.09
US 1016 (5 families)	655	24	424	231	24	0.23	<0.01	<0.01	<0.01
US 1017 (4 families)	604	21	365	239	21	0.38	<0.01	<0.01	<0.01
US 1018 (3 families)	215	18	134	81	18	<0.01	<0.01	0.74	0.07
US 1019 (3 families)	83	6	48	35	6	0.02	<0.01	0.59 (0.94*)[y]	0.72
US 1020 (6 families)	242	9	172	70	9	0.44	0.06	0.01	<0.01
Half-sib total	2029	89 (≈23:1)	1263	766	89	<0.01	<0.01	<0.01	<0.01
2004 Backcrosses									
US 1016 × G-176	9	5	4	5	5	0.06[x]	0.04	0.29	<0.01
US 1017 × G-176	61	2	38	23	2	<0.01	<0.01	<0.01	<0.01
Backcross total	70	7 (10:1)	42	28	7	0.07	<0.01	<0.01	<0.01
2005 half-sib crosses									
US 1016 (1 family)	53	1	50	3	1	0.68	0.01	<0.01	0.08
US 1018 (4 families)	207	6	164	43	6	0.97**	0.77	<0.01	<0.01
US 1019 (5 families)	73	10	49	24	10	<0.01	<0.01	0.22	0.05
US 1020 (4 families)	64	3	51	13	3	0.40 (0.95**)[y]	0.62 (0.97**)[y]	0.25	<0.01
US 1028 (4 families)	120	27	79	41	27	<0.01	<0.01	<0.01	<0.01
US 1039 (3 families)	149	31	75	74	31	<0.01	<0.01	<0.01	0.01 (0.97**)[y]
US 1040 (4 families)	195	62	100	95	62	<0.01	<0.01	<0.01	<0.01
US 1041 (4 families)	222	56	94	128	56	<0.01	<0.01	<0.01	<0.01
Half-sib total	1083	196 (≈6:1)	662	421	196	<0.01	<0.01	0.01 (0.90**)[y]	<0.01
2005 Backcrosses									
US 1016 × G-176	23	3	16	7	3	0.48[x]	<0.01	<0.01	NA[w]
US 1019 × G-176	13	0	7	6	0	0.11	<0.01	<0.01	NA
US 1020 × G-176	7	4	3	4	4	0.08	0.09	0.37	NA
US 1040 × G-176	10	2	3	7	2	1.00**	0.73	0.02	NA
Backcross total	53	9 (≈6:1)	29	24	9	0.65	<0.01	<0.01	NA

[z]The highest probability within each row (cross) is in italic if over at least P > 0.10.

[y]Values in parentheses represent significant χ² values derived for an individual family within the female parent grouping. All other individual family values were not significant.

[x]The parental compositions tested in backcrosses are duplex × nulliplex and simplex × nulliplex crosses, respectively.

[w]NA = not applicable. In a simplex × nulliplex cross in this model, only the diminished seed class and the parthenocarpic classes are expected to segregate. The seeded types that segregated in this cross cannot be tested against the model expectations.

a 27:8:1 segregation of normal:diminished:parthenocarpic would be expected (Fig. 1). Both duplex × duplex and duplex × simplex possibilities were examined for each model (Table 3).

No single model fit the data well. For the 1993 data (with only two classes), none of the χ²s were statistically significant. Several backcrosses approached significance, but the size of these families was quite small. Similarly, in the 2004 and 2005 data, only a few crosses under any of the parental type or model assumptions were significant. Summation values across all half-sibs or backcrosses also had low probability values. In 2004, the summed ratio of seeded to parthenocarpic types was ≈23:1 for half-sib families and 10:1 for backcrosses. In 2005, the summed ratio across half-sib families was ≈6:1 (as a result of an increased relative number of parthenocarpic types) and the ratio across backcrosses was also ≈6:1. A possible explanation for the 2005 half-sib family results was that it was a poorer pollination year, and perhaps plants that would have been considered diminished-seed phenotypes in some years exhibited a parthenocarpic phenotype. The families evaluated in 2004 were (for the most part) different from those in 2005, preventing simple comparisons of year effects; however, several parents were common to both years; these were US 1018, US 1019, and US 1020. In half-sib groupings, these clones exhibited seeded-to-parthenocarpic ratios in 2004 and 2005, respectively, of 13.7 and 34.5 (US 1018), 10.3 and 9.7 (US 1019), and 25.0 and 27.6 (US 1020). Thus, US 1018 varied widely between years, whereas the other two selections varied to a lesser degree. Interpreting the specific and general results from segregating families, it appears that this trait can have considerable environmental interaction.

Although tests of fit to either model were generally nonsignificant, they described the observed segregations better than other alternatives that were considered. Permutations of the incomplete dominance model that shifted the boundaries of genotype dosages defining different categories did not improve model fit nor did a model based on lethality of homozygous recessive types (models and analysis not shown).

Although the precise nature of the genetic control was unclear, it was not difficult to recover parthenocarpic types from most families. There were exceptions to this; for example, five of six crosses evaluated in 2004 having US 1020 as a female parent produced no parthenocarpic types (individual family data not shown). There was little support for a diminished seed phenotype as described in the incomplete dominance model. This may arise from subjective judgments categorizing normal seed versus diminished seed types. Alternatively (but less likely), the diminished seed type may be a variant type within this germplasm, related to self-fertility, but not associated with the parthenocarpic trait per se. Nonetheless, we felt it was not difficult to recognize diminished seed types, and they
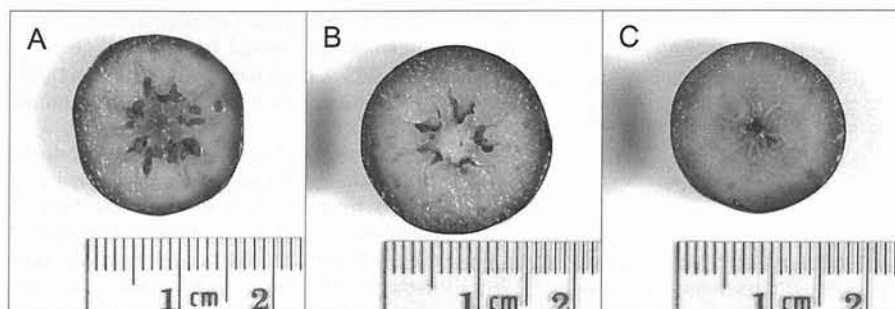
Fig. 2. Ranges of seed development expressed in families segregating for parthenocarpy (**A**) normal, (**B**) diminished seed type, (**C**) parthenocarpic type.

often exhibited better fruit production than the true parthenocarpic types. It may be argued that the parthenocarpic trait has incomplete penetrance and that diminished seed types *are* parthenocarpic types that have simply had better pollination and therefore better fruit set.

Inbreeding effects may also play a role in our results. Inbreeding depression appears to be the reason for limited family sizes in the backcrosses, and although G-176 was specifically crossed into a wide diversity of backgrounds, inbreeding effects associated with the parthenocarpic trait (or some other genetic aspect of G-176) may play a role in what was observed in the half-sib families.

Conclusion

Parthenocarpy is heritable but does not fit a simple genetic model. Some selections in segregating families exhibited true parthenocarpy; however, the conditions necessary to achieve a widespread expression of this trait in all buds, yielding an economically competitive parthenocarpic crop, were not apparent (i.e., in many cases, the total fruit set and yield were far below what might be expected if parthenocarpy were to live up to its maximum possibilities). The reduced yield of parthenocarpic clones suggests that this material in its present form will not solve all the pollination problems discussed previously, but may be most useful, initially, in the plants expressing diminished seed development. This variant appears to enhance fruit development and reduce seed development, producing higher pulp-to-seed ratios, and may allow more fruit development with minimal pollination. It should also improve fruit quality by this overall reduction of seed development. Additional cycles of recombination and selection are currently underway in this material. If our understanding of diminished seed types is clarified by further crosses, these variants might allow easier recognition and recovery of plants exhibiting better levels of expression of parthenocarpy. In 2005, crosses were made of diminished seed types to standard cultivars, to other diminished seed types, and to parthenocarpic types to further investigate genetics and recovery of this trait and to further build

breeding populations. These crosses should provide a further test of this model.

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